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**BONTE, D.**, HOVESTADT, T. & POETHKE, H.-J. (2010).

Oikos 119: 560-566



**BONTE, D.**, HOVESTADT, T. & POETHKE, H.-J. (2010). Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119: 560-566.
**Doi:** 10.1111/j.1600-0706.2009.17943.x

# Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes

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**Abstract**

Many organisms show polymorphism in dispersal distance strategies. This variation is particularly ecological relevant if it encompasses a functional separation of short- (SDD) and long-distance dispersal (LDD). It remains, however, an open question whether both parts of the dispersal kernel are similarly affected by landscape related selection pressures.

We implemented an individual-based model to analyze the evolution of dispersal traits in fractal landscapes that vary in the proportion of habitat and its spatial contagion. Individuals are parthenogenetic with dispersal distance determined by two alleles on each individual's genome: one allele coding for the probability of global dispersal and one allele coding for the variance $\sigma$ of Gaussian local dispersal with mean value zero.

Simulations show that mean distances of local dispersal and the probability of global dispersal, increase with increasing habitat availability, but that changes in the habitat's spatial autocorrelation impose opposing selective pressure: local dispersal distances decrease and global dispersal probabilities increase with decreasing spatial autocorrelation of the available habitat. Local adaptation of local dispersal distance emerges in landscapes with less than 70% of clumped habitat.

These results demonstrate that long and short distance dispersal evolve separately according to different properties of the landscape. The landscape structure may consequently largely affect the evolution of dispersal distance strategies and the level of dispersal polymorphism.

## Introduction

Dispersal has important ecological and evolutionary consequences for organisms living in spatially structured populations (Kokko & López-Sepulcre 2006). It plays therefore a crucial role in the context of habitat fragmentation. Dispersal has repeatedly been shown to be a plastic process conditional on the individual's social and ecological environment (Clobert et al. 2009). Further, the presence of heritable variation and strong selection pressures related to e.g. landscape composition may induce fast evolution in dispersal traits (for reviews see Bowler & Benton 2005, Kokko & López-Sepulcre 2006, Ronce 2007). The dispersal strategy should be considered as an integrated process, encompassing dispersal propensity as well as transfer and settlement, the latter two being reflected in an individual's effective displacement distance.

Three kinds of mechanisms have been shown to favor the evolution of increased dispersal rates: kin competition (e.g., Hamilton & May 1977, Frank 1986, Taylor 1998, Ronce et al. 2000, Poethke et al. 2007), inbreeding avoidance (e.g., Waser et al. 1986, Gandon 1999) and environmental stochasticity in space and time (e.g. Van Valen 1971, Olivieri et al. 1995, Friedenberg 2003, Poethke et al. 2003). Evidently, these benefits are balanced by intrinsic or landscape-related dispersal costs (e.g., McPeek & Holt 1992, Travis & Dytham 1999, Heino & Hanski 2001, Poethke & Hovestadt 2002, Poethke et al. 2003). Although the evolution of dispersal distance has received far less attention, the available studies (Rousset & Gandon 2002 for kin competition, Hovestadt et al. 2001 for relationship with dispersal mortality, Murell et al. 2002 for correlations with subpopulation dynamics), point out that mechanisms that act on the evolution of emigration rates may equally affect the evolution of dispersal distance. It is therefore reasonable to assume that the spatial extent of these selective forces will affect the evolution of increased dispersal distances as well. Because dispersal propensity and dispersal distance determine gene-flow, they may strongly interfere with, and often constrain, processes of local adaptation and trait polymorphism in natural landscapes (Lenormand 2002, Billiard & Lenormand 2005, Garant et al. 2007). Thus, dispersal may be subject to local adaptation (Hovestadt et al. 2001, Gros et al. 2006) and may, at the same time, influence spatial patterns in local adaptation and its evolution.

Many organisms show polymorphism in dispersal distance strategies. Animals may disperse by different mechanisms in the larval life phase compared to the adult stage (Ghent 1999, Bonte et al. 2007). Many anemochorous (i.e., wind dispersed) plants show distinct seed dimorphism with heavy short-distance dispersing seeds and light seeds with pappus-structures for long-distance aerial dispersal (Imbert 2001, Cheptou et al. 2008), may 'exploit' different dispersal vectors like birds with small and large home-ranges, or plants may either distribute clonally by stolones or by seeds (e.g., Gardner & Mangel 1999).

The dispersal polymorphism is of particular ecological relevance if it encompasses a functional separation of short- and long-distance dispersal (further on abbreviated as respectively SDD and LDD). Presumably, such different dispersal modes are characterised by different cost-benefit ratios due to evolutionary and environmental constrains (Bonte et al. 2006). Therefore different parts of the dispersal kernel may evolve independently (Ronce 2007, Bonte et al. 2008). For instance, long distance dispersal (i.e., dispersal beyond the bounds of the local habitat cluster) can be considered to be most advantageous in landscapes with high habitat availability or under conditions with strong enemy interactions (Hovestadt et al. 2001, Muller-Landau et al. 2003).

At large spatial scales, we can expect that polymorphisms in dispersal strategies are maintained by among-landscape variation in environmental stochasticity, habitat quality and dispersal mortality. Even at smaller spatial scales, i.e. within metapopulations, polymorphism in dispersal may evolve as a consequence of local adaptation towards local habitat configuration. This was empirically demonstrated by Hanski et al. (2004) and Bonte et al. (2006). These fast evolutionary responses towards local landscape structure are important for species conservation because they may either rescue or hasten species extinction through genetic and demographic feedbacks. This has for instance been shown by Colas et al. (1997) for an extremely rare, endemic cliff-dwelling plant species. Within single patches of habitat, recent modelling work (Gros et al. 2006) suggests that local adaptation in dispersal strategies may only evolve beyond a minimum patch size at the edges of patches.

While insights into dispersal evolution are predominantly delivered by modeling and microcosm experiments in simple landscapes, field studies highlight the importance of landscape structure for dispersal evolution (e.g., Hill et al. 1999, Hanski et al. 2004, Bonte et al. 2006, Merckx & Van Dyck 2006, Schtickzelle et al. 2006, Bonte et al. 2007, Cheptou et al. 2008). According to this empirical work, low dispersal distances in habitat embedded in hostile matrix (isolated habitat, edges) and high dispersal distances in continuous habitat are hypothesised to be an adaptation to the local landscape structure. Our understanding of dispersal evolution and the environmental conditions for local dispersal adaptation within realistic landscapes needs consequently to be bridged by theoretical studies. Therefore, we developed a spatially explicit, individual based model for dispersal in fractal landscapes differing in their degree of habitat availability and habitat clumping (With & King 1997). These are useful to assess the evolution of dispersal distance in a conceptual, though realistic way (With 1997). We explicitly address the question how changes of both, habitat availability and its spatial autocorrelation or contagion affect the evolution of dispersal distance polymorphism, by inferring dispersal kernels that are a function of two different dispersal functions. In contrast to earlier theoretical work (Hovestadt et al. 2001, Murell et al. 2002, Rousset & Gandon 2002), we here explored under which landscape configurations adaptive polymorphisms in dispersal distance strategy emerge.

## Material and Methods

### Neutral landscapes

We used the program QRULE (Gardner 1999, Gardner & Urban 2007) to generate spatially structured landscapes. The generated landscape models are binary (i.e., only with a binary distinction between suitable habitat and unsuitable matrix) and measure 256 x 256 grid cells. For details on the landscape generator algorithm we refer to Gardner (1999). In short, we used fractal landscapes that are generated using the mid-point displacement algorithm in which both the fraction (*P*) and the degree of spatial autocorrelation (*H*) can be controlled. *H* represents the spatial autocorrelation or clumping of habitat, with low values indicating dispersed distribution of habitat cells; high values represent a strongly aggregated habitat distribution (With 1997). It should be noted that such fractal landscapes are always clumped and never overdispersed as compared to a pure Poisson process. Nevertheless we will use the term "clumped" for highly autocorrelated (large values of H) and "dispersed" for less autocorrelated (low H) landscapes. Fig. 1 provides examples of four landscapes differing clumping (*H)* and fraction of suitable habitat (*P).* Fractal landscapes provide a tool to tease apart the effects of habitat fragmentation (with high values of *H* indicating strong connectivity) from habitat loss (with high values of *P* indicating high amounts of preserved habitat). To avoid edge effects in the simulations, landscapes were wrapped at the edges into a torus so that edges matched, and can consequently be considered as being infinite but periodic landscapes.

We investigated the evolution of dispersal distance in fractal landscapes that systematically varied in *P* between 0.1 and 0.9 and *H* between 0 and 1 (Table 1). Intervals were 0.1 in both cases, subsequently resulting in 99 landscapes with different combinations of *H* and *P.* We chose to generate 5 replicates of 99 interdependent landscape (the landscapes are generated from the same baseline fractal landscape; Gardner 1999). Consequently, a total of 495 simulations (described hereunder) were run.

### The model

***Individuals*** **-** We modelled the evolution of dispersal distance in parthenogenetic organisms with discrete generations. Individuals either disperse globally with a certain probability (i.e., the individual

is displaced toward a random cell in the landscape), or they draw a distance from a Gaussian probability distribution (see below). We chose to implement this dispersal function because (i) it allows the generation of fat-tailed dispersal kernels by increased global dispersal and (ii) because of its realism in many terrestrial arthropods with polymorphic dispersal strategies (Zera & Denno 1997). Dispersal costs emerge in first instance due to arrival in unsuitable matrix cells, but we alternatively tested a scenario with additional distance dependent dispersal mortality $\mu_{disp}$. The latter is positively linearly correlated with dispersal distance according to the rule $\mu_{disp}$=dist/$dist_{max}$. In our landscape of 256 x 256 grids, $dist_{max}$ equals 362.

***Local population dynamics –*** Each habitat grid cell was characterised by a carrying capacity *K* beyond which reproduction failed (table 1). Reproduction takes place after dispersal, i.e. after the building-up of local densities ($\delta$). The realised number of offspring $\lambda$ was determined as a linear function of the local density $\lambda=K/\delta$, with complete loss of individuals through failed reproduction when $\delta >= K$ in local grid cells, but with the possibility for recolonization from reproducing individual in the landscape. Individuals die immediately when they disperse into the hostile matrix. These local population dynamics resemble typical arthropod herbivores with distinct genetically determined dispersal polymorphism and scramble competition (Zera & Denno 1997).

Alternatively, we tested the model for logistic growth population dynamics (i.e. contest competition), hypothesised to plant systems. Therefore, we modified local population dynamics according to Hassell & Comins (1976). Local population dynamics are governed by density-dependent reproduction of individuals. Each generation, a female gives birth to $\Lambda$ offspring, where $\Lambda \sim$ Pois($\lambda$). In our simulations, $\lambda$ was set to 2, typical for arthropod demography (Bellows 1981). Offspring develop into mature individuals with a density-dependent survival probability *s* due to contest competition:

$$s = \frac{1}{(1 + a\delta)} \qquad (1) \qquad \text{with } a = \frac{\lambda - 1}{K}$$

Here $\delta$ represents the local population density and *K* carrying capacity.

***Evolution of dispersal –*** Dispersal distance is determined by two alleles on each individual's genome: one allele (allele $G_p$) coding for the probability of global dispersal $p_{global}$. Alternatively, that is with probability 1- $p_{global}$ individuals will disperse locally according to a Gaussian dispersal kernel (mean value of 0) with the genetically determined variance ($\sigma$). The Gaussian kernel is two-dimensional with randomly selected directionality. Thus the second allele ($G_g$) codes for the variance ($\sigma$) of the Gaussian distribution. $G_p$ Individual allele frequencies were initialised from a uniform distribution [0..1], and for $G_g$ from a uniform distribution [1..128]. Offspring inherit both alleles from their parent, but alleles may mutate with a probability of 0.001. Mutations are uniformly sampled within the interval 0.9•x to 1.1•x. As a consequence, all individuals are theoretically dispersing, but philopatry (dispersal with distance zero) occurs when both $G_p$ and $G_g$ approach zero.

**Data analysis**

Stable distributions of trait values were reached within 1000 time-steps in all scenarios. Mean trait values were calculated for all surviving individuals in one landscape. Beyond the global evolutionary results we were also interested to investigate under which conditions local adaptation of dispersal traits can occur. To characterize local conditions, we estimated the proportion habitat cells ($p'$) in the vicinity of 1000 randomly selected habitat cells in a similar way as the developed univariate O-ring statistics by Wiegand et al. (1999). The number of suitable habitat cells in 100 increasing radii of 1 grid cell was counted for each of these randomly selected cells. In a fractal landscape the availability of habitat is expected to more or less gradually decline with distance for any cell of suitable habitat, ultimately equilibrating at the proportion of available habitat in the entire landscape ($P$). We use the slope $\alpha$ of the fitted negative exponential function $p'=e^{-(\alpha \bullet radius)}$ to describe the change in habitat availability with distance for the individual cells, with high values representing steeply declining availability (as would be the case for isolated patches in the landscape, or patches at edges of clumped habitat cells). Intermediate values of $\alpha$ indicate gradually declining habitat availability, while values of $\alpha$ close to 0 would indicate a homogeneous habitat distribution within the landscape sector analyzed. In a region with rapidly declining habitat availability (large $\alpha$) it should be beneficial to limit local dispersal to the near vicinity, i.e. selection should favour low levels of the allele $G_g$. We thus use

the strength of the Spearman rank correlation ($R_s$) between the cell's value for $\alpha$ (a habitat attribute) and the values of the two dispersal alleles ($G_p$ respectively $G_g$) of the individual residing in this cell to estimate the degree of local adaptation (or selection driven polymorphism). We assume the presence of local adaptation only when $R^2_s > 10\%$.

Mean individual trait values and Spearman correlations between local trait values and local landscape structure were subsequently averaged over the five independent replicas for each landscape type (i.e., each landscape determined by one of the 99 *H,p*-values). These averaged trait values are presented in this contribution.

**Results**

Evolutionary stable Gaussian dispersal distances (Fig 2 A,C,E) evolve towards higher values with an increase in the proportion of available habitat (*P*) as well as with an increase in spatial autocorrelation (*H*). The proportion of individuals performing global dispersal also increases with increasing *P* but declines with increasing *H* (Fig. 2B,D,F), i.e. selection favours the investment into local dispersal as autocorrelation becomes larger (at a given overall habitat availability). We thus observed the prevalence of more fat-tailed dispersal kernels due to increased global dispersal in landscapes characterized by more evenly distributed suitable habitat. The obtained outcome is consistent over the three different simulation experiments (Fig 2) and does, with exception of a slight decrease in global dispersal, not depend on the applied submodels for local population dynamics or the implementation of distance dependent dispersal mortality. Neither did we detect deviations in scenarios with different $\lambda$ or *K* (results not shown).

No local adaptation within landscapes was recorded for global dispersal trait values (all $R^2<0.03$). However, local adaptation in the Gaussian component of dispersal emerge when the availability of habitat *P* falls below 0.7 and when at the same time clumping is high (*H* within range 0.4-1 (Fig. 3, only data presented for simple scramble competition). These ranges of landscape structure correspond with the evolution of local dispersal distances (trait $G_g$) in the range of 1.5-3 units (Fig 2A).

**Discussion**

The availability of habitat and its spatial distribution has a prominent effect on the evolution of dispersal distances. We show that an increasing proportion of suitable habitat in a landscape selects – unsurprisingly – for increased dispersal distance, as reflected by the increased investments into global dispersal and the parallel increase in the local dispersal distances. Yet a change in autocorrelation inflicts opposing selective pressure on the local and global component of dispersal. This gives rise to particularly fat-tailed dispersal kernels under conditions of spatially uncorrelated habitat availability (large fraction of global dispersal but short mean dispersal distance for local dispersal). Polymorphism in dispersal tactics only emerged in landscapes with low habitat availability and high spatial autocorrelation and emerged only with respect to the trait coding for the Gaussian dispersal tactics. This local adaptation emerged in landscapes that select against global dispersal and for intermediate Gaussian dispersal rates, i.e. in landscapes with less than 70% but strongly clumped habitat.

The retrieved patterns are obviously relevant for organisms with mixed dispersal strategies encompassing (i) more or less controlled short distance dispersal (SDD) and (ii) uncontrolled passive long distance dispersal (LDD). These conditions hold for seed dimorphic plants with investments for anemochorous dispersal, insects with facultative wing formation like aphids and some butterflies, arthropods that use silk as a dispersal mode and probably many organisms that combine passive, uncontrolled dispersal phases with more active dispersal modes. Neither the implementation of local logistic growth with contest competition nor the distance dependent dispersal mortality affected this pattern. Because we implemented asexual reproduction and low local carrying capacities, strong kin competition can here be attributed to overrule the expected decreasing dispersal under logistic growth or additional dispersal mortality (Hamilton & May 1977; Ronce et al. 2000; Poethke et al. 2007).

The few empirical studies that detected a geographic variation in dispersal tactics confirm our theoretical predictions that (passive) LDD would be advantageous in landscapes with high degrees of habitat availability (Imbert 2001; Cody & Overton 1996; Bonte et al. 2006, 2007; Cheptou et al.

2008), but no evidence for shifts towards more controlled movement methods in highly connective landscapes were found. To our knowledge, no empirical studies have explicitly tested the relationship between spatial configuration and the evolution of dispersal polymorphism within heterogeneous landscapes. However, if we consider detectable movements of butterflies as short distance dispersal that contrast with probable, but rarely quantified long distance dispersal (Van Dyck & Baguete 2004), patterns found in a meadow-inhabiting species (Baguette & Schtickzelle 2006) fit our predictions.

Because our model deals with the evolution of ecological phenomena typical for passively dispersing organisms, we hypothesised the polymorphism to be adaptive within a landscape if distances decrease with increased habitat isolation and availability (Bonte et al. 2007; Cheptou et al. 2008). Evidently, different responses can be expected for actively moving organisms with certain habitat detection abilities (Lima & Zollner 1996). In first instance, our simulations point out the absence of local adaptation in LDD dispersal strategies. This is not unexpected given the overall low dispersal rates, rendering the trait more subject to drift than to selection, and the simultaneous gene flow over very large distances associated with this mode of dispersal. In contrast, local adaptation in Gaussian dispersal distance was detected in landscapes with high degrees of autocorrelation and habitat availability up to 70%. These comprise landscapes that on average select for intermediate dispersal distances and accord with earlier theoretical work on the relationship between gene flow and local adaptation (Lenormand 2002; Billiard & Lenormand 2005; Garant et al. 2007). Because dispersal distance is expected to be tightly related to gene-flow, extremely low dispersal distances will lead to the absence of gene flow and consequently low genetic variation on which natural selection can act. In contrast, high levels of gene flow through large dispersal distances will be responsible for gene swamping. High dispersal distances will consequently erode any emergence of local adaptation in dispersal distance.

By modelling combined dispersal kernels, we show that different parts of the kernel (i.e., SDD and LDD) are affected by different landscape-related selection pressures. Both SDD and LDD consequently evolve independently, despite the simplicity of the applied simulations. Moreover, it can be expected that the consideration of (i) different associated dispersal costs and (ii) additional

environmental attributes like different rates and spatial extents of disturbance (Muller-Landau et al. 2003) will presumably amplify these independent evolutionary mechanisms.

Given the relevance of LDD for biological invasions (Muller-Landau et al. 2003) and range expansion under climate change (Phillips et al. 2008), we can expect serious geographic variation in range expansion rates for species with distinct dispersal polymorphisms. This geographic variation is expected to be related to the landscape configuration of source populations with larger range expansion fronts for those populations, inhabiting landscapes with high levels of naturally or already long-term fragmented habitat. Evolutionary responses of dispersal kernels at range expansion fronts are documented (Travis & Dytham 2002, Phillips et al. 2008). Our simulations additionally point out that the underlying landscape structure should be equally considered when predicting invasive range expansion of species under global change.

**Acknowledgements**

DB received a mobility grant from the Fund for Scientific Research – Flanders (FWO) for a long-term stay at Würzburg University. DB was funded by FWO research grant (G.0057.09). HJP and TH are partially supported by a grant from the "Deutsche Forschungsgemeinschaft" (DFG PO244/4).

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1 Table 1 – Summary of the model parameters

2

| Parameter | Description | Ranges tested (sensitivity analysis) |
|---|---|---|
| $K$ | Carrying capacity local populations | 5 (7,10,30*) |
| $\lambda$ | mean offspring number (logistic growth submodel) | 2 (3,4,5) |
| $\mu$ | dispersal mortality (distance dependent mortality submodel) | $dist/dist_{max}$ |
| *P* | Proportion of available habitat in the landscape | 0.1,0.2,….0.9 |
| *H* | Spatial autocorrelation of the available habitat | 0,0.1,0.2,…1 |

3 *: analysis done in grid landscape of 128 x 128 cells for computational reasons

4

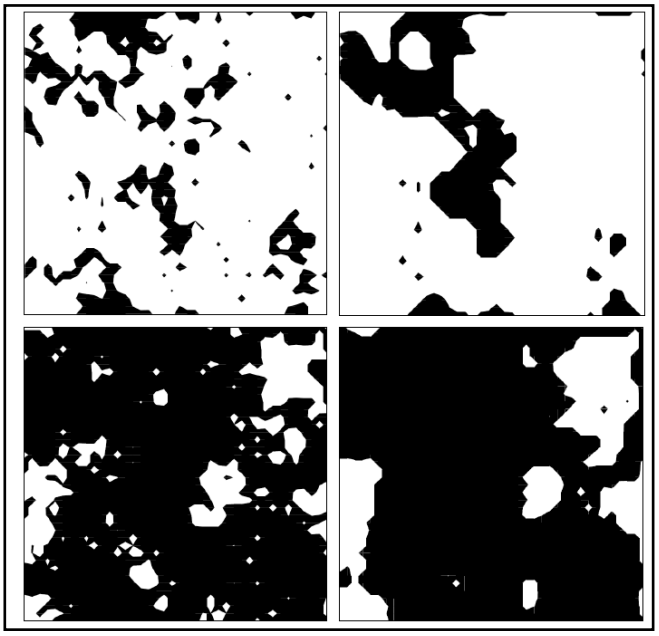
**Figure Legends**

**Figure 1 – Examples of fractal landscapes used in simulations. Upper panels contain P=0.2 habitat (black), lower panels P=0.8. Left panels show a more dispersed distribution (H=0.2), right ones are more clumped (H=0.8).**

**Figure 2 - Mean values for dispersal traits according to the proportion of available habitat (P) and its degree of autocorrelation (H). A,C,E: Mean value of the allele for the Gaussian distance, B,D,F: frequency of individuals performing global dispersal. We present data for respectively the baseline smodel (scramble competition; A,B), logistic growth model (C,D) and baseline model with distance dependent dispersal mortality (E,F).**

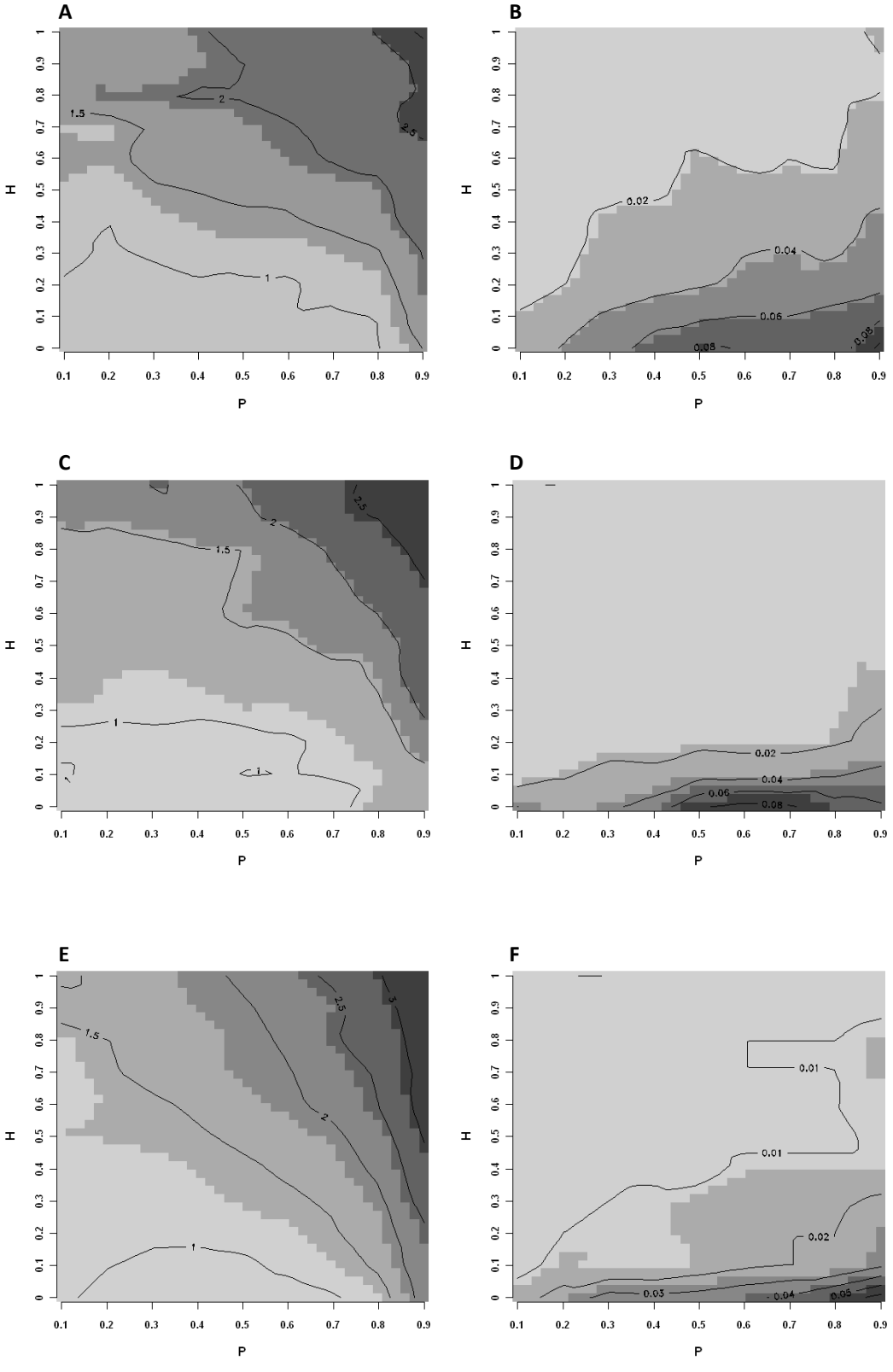
**Figure 3 - A. Strength of local adaptation ($R^2$, see material and methods for details) of Gaussian dispersal distance strategies according to the proportion of available habitat (*P*) and its degree of autocorrelation (*H*).**

1 **Figure 1 -**



2

1 **Figure 2 -**




2

3

4

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**Figure 3 -**